REPRODUCTIVE STRUCTURES AND EVOLUTION IN LUDWIGIA (ONAGRACEAE). I. ANDROECIUM, PLACENTATION, MERISM¹

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ABSTRACT

This article, based on serial sections from 19 species of Ludwigia (supplemented where necessary with preparations from other Onagraceae), begins an effort to outline the evolution of flower, fruit, and seed characters within the genus and to link the outline with what is known of floral evolution elsewhere in the family. New observations include the following: all Ludwigia anthers have a prominent endothecium, and developing anthers of certain advanced species are markedly H-shaped in cross section; pollen of two species matures in isolated packets; ovules of L. leptocarpa, though commonly 1-seriate, can be distally pluriseriate; only rarely does a Ludwigia placenta have a median groove suggesting paired carpel margins. The deeply intrusive placentas seen in section Myrtocarpus, but lacking in some of the other sections, are probably ancestral, and the old idea that diplostemony and 4+-mery are ancestral holds up well when reexamined critically.

Few families have been as intensively studied by evolutionary botanists as the Onagraceae. Relationships among many infraspecific variants and among closely connected species groups have been firmly established through cytological work, breeding experiments, and field observations of reproductive events. As one proceeds to more widely separated taxa, however, biosystematic methods become inapplicable; consequently, evolutionary links among the genera of Onagraceae are not yet well understood. Structural comparison remains the bestperhaps the only—way to improve our knowledge of these links. First, structural differences among the taxa must be identified, then the direction of evolutionary change can be inferred by critically weighing the alternatives. The Onagraceae are ideal in several respects for comparative studies of floral structure. For one thing, the family is of manageable size: Raven currently recognizes 17 genera and estimates the number of species to be 600-700. "Spirit collections" of many of these species are available for anatomical work because of the research efforts of Raven and his collaborators. Another advantage in working with Onagraceae is that the taxa are diverse enough to be challenging, yet undoubtedly of common evolutionary origin. Among the characters that show the Onagraceae to be a natural family are the peculiar viscin threads on onagraceous pollen (Skvarla et al., 1977) and the distinctive 4-nucleate embryo sac (Seshavataram, 1970; Bhatnagar & Johri, 1972:91; Palser, 1975:641). Still another advantage is that the nearest extra-familial affinities of the Onagraceae are known to be among the myrtalean families Combretaceae, Crypteroniaceae, Lythraceae, Melastomataceae, Myrtaceae, Punicaceae, and Sonneratiaceae. Similarities in floral structure within this alliance were recognized by pre-Darwinian taxonomists and are now seen as indicators of shared ancestry, with strong con-

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firmatory evidence from such diverse sources as embryology (Subramanyam, 1951) and vegetative anatomy (Carlquist, 1975; van Vliet, 1975; van Vliet & Baas, 1975). Ideas on "ancestral versus derived" in the Onagraceae can be tested by looking into the related families for satisfactory distribution of the putative ancestral state.

Though the ultimate goal is to understand the evolution of the Onagraceae as a whole, this report concentrates on Ludwigia L., the only genus of the tribe Jussiaeeae (Raven, 1963). More than 70 species are known, all from wet habitats in temperate and tropical regions around the world (for illustrations, see Micheli, 1875; Rickett & Collaborators, 1967; Correll & Correll, 1972). Various authors have considered Ludwigia-or Jussiaea, now a synonym of Ludwigia-the primitive onagraceous genus (see Melchior, 1964; Takhtajan, 1966, 1973) because it seemed to provide the best link with adjoining families and because Ludwigia flowers were thought to retain ancestral traits, among them the 5(or more)merous condition and the absence of a floral tube beyond the inferior ovary. It now seems that the absence of a floral tube is secondary in this case; moreover, it is now recognized that Ludwigia has a derived basic chromosome number and other specialized features. Undoubtedly, however, the genus represents an early evolutionary offshoot within the Onagraceae; a credible phylogenetic outline of the family must account for its peculiarities. My wet material of Ludwigia, flowers from 30 collections belonging to 19 species, is listed in Table 1 along with nine collections from five more species (asterisked) that were available only as herbarium specimens. Altogether, these collections represent 10 of the 17 infrageneric sections recognized by Raven in 1963. Stained serial cross sections were prepared from all the collections and replicate series from most, also longitudinal series as needed, bringing to more than 100 the number of flowers (and developing fruits) sectioned and examined. Thanks to Raven and his collectors, I was able to compare the sectioned Ludwigia flowers with sectioned flowers from more than 70 additional species of Onagraceae, systematically selected from all parts of the family. I begin with the androecium, though I have few new observations on Ludwigia stamens, because I want an unequivocal basis for discussing character associations, and I think all systematic botanists, despite differences in training and philosophical outlook, will accept the evidence for ancestral diplostemony in Ludwigia.

ANDROECIUM

In general, Ludwigia species are constantly diplostemonous (the old genus Jussiaea, Fig. 1) or constantly haplostemonous (Fig. 2), but L. perennis can be intermediate (Raven, 1963), and at least one species, L. inclinata, includes some plants with two whorls of stamens, others with one whorl (Raven, personal communication). One may be confident that diplostemony is the ancestral condition because of its wide distribution in the Onagraceae, haplostemony occurring (outside Ludwigia) only in two genera with highly specialized flowers (Circaea, Lopezia) and in specialized members of two other genera (one species of Camissonia, sect. Eucharidium of Clarkia). In neighboring families, stamens are

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TABLE 1. Herbarium vouchers for sectioned Ludwigia flowers.^a

Taxa	Vouchers
Sect. Oligospermum	
L. peploides (H.B.K.) Raven	Raven 14529 (LA), California. Raven 26493 (MO), Arkansas.
L. uruguayensis (Camb.) Hara	Raven s.n. (DS), California [Naturalized, Stanford Univ.].
Sect. Oocarpon	
*L. torulosa (Arnott) Hara	Cowan 38886 (US), French Guiana. de la Cruz 3813

Sect. Nipponia *L. epilobioides Maxim. Sect. Seminuda

L. leptocarpa (Nutt.) Hara

Sect. Fissendocarpa *L. hyssopifolia (G. Don) Exell

Sect. Myrtocarpus L. decurrens Walt.

> *L. densiflora (Mich.) Hara L. erecta (L.) Hara L. foliobracteolata (Munz) Hara L. latifolia (Benth.) Hara L. peruviana (L.) Hara *L. tomentosa (Camb.) Hara

(US), Guyana. Howara & Howara 9911 (US), Dominican Republic.

Chien 207 (US), China.

Chevalier 21 (DUKE), Florida. Raven 26491 (MO), Arkansas.

Asplund 14132 (US), Peru. Purpus 6973 (US), Mexico.

Broome 855, 896 (both DUKE), North Carolina. Raven 26469 (MO), Arkansas. Macedo 3940 (US), Brazil. Raven 21573 (DS), Costa Rica. Raven 21981 (DS), Costa Rica. Raven 21575 (DS), Costa Rica. Steinberg s.n. (FAU), Florida. Dawson 15154 (RSA), Brazil. Gardner 2571 (US), Brazil.

Sect. Macrocarpon

L. neograndiflora (Munz) Hara L. octovalvis (Jacq.) Raven Sect. Ludwigia L. alternifolia L. L. maritima Harper

L. virgata Michx.

Sect. Microcarpium L. alata Ell. L. glandulosa Walt. L. linearis Walt. L. pilosa Walt. Sect. Dantia L. arcuata Walt. L. palustris (L.) Ell. Krapovickas & Cristóbal 12089 (DS), Paraguay. Raven 21574 (DS), Costa Rica.

Broome 851, 860, 862 (all DUKE), North Carolina. Chevalier 18 (DUKE), Florida. Arguelles 1 (MO), Mississippi. Broome 863 (DUKE), North Carolina. Willingham 597 (MO), Georgia.

Arguelles 3 (MO), Mississippi. Broome 865 (DUKE), North Carolina. Broome 856 (DUKE), North Carolina. Broome 861, 902 (both DUKE), North Carolina.

Chevalier 11 (DUKE), North Carolina. Broome 859 (DUKE), North Carolina. Willingham 598 (MO), Georgia. Arguelles 2 (MO), Mississippi.

^a Asterisks mark species for which herbarium flowers were sectioned; for other species, liquid-preserved flowers were used.

commonly twice or more than twice the number of sepals, the haplostemonous exceptions being the apetalous genus Crypteronia, the myrtaceous genus Myrrhinium (with specialized inflorescences and stamens; McVaugh, 1968: 407), and certain members of the families Lythraceae and Melastomataceae. The androecia of Lythraceae are almost bewildering in their meristic diversity; how-



FIGURES 1-2. Ludwigia illustrations.—1. L. leptocarpa. Top of plant (a). $\times 0.3$. Flower (b). $\times 1.7$.—2. L. linearis. Top of plant (a). $\times 0.3$. Flower (b) and fruit (c). $\times 3.3$. Partly

redrawn by A. Tangerini from illustrations prepared by G. Reinert for R. K. Godfrey, who kindly lent the originals for copying.

ever, the fact that some of the haplostemonous taxa have stamens opposite the petals and others have stamens opposite the sepals is best explained by deriving both forms from precursors with at least two whorls of stamens. In the Melastomataceae, haplostemony is very much a minority trait, but a widely scattered one, occurring in seven New World genera (Wurdack, 1971: 360) and at least

five Old World genera: *Blastus*, *Dactylocladus*, *Dissochaeta*, *Omphalopus*, and *Sonerila*. I am assured by melastome specialist J. Wurdack that this taxonomic distribution indicates multiple evolutionary derivation of haplostemony within the family. Returning to the Onagraceae, we find in the genus *Ludwigia* itself that the woodier tropical species are mostly diplostemonous, whereas temperate species with such advanced features as poricidal capsules or apetaly are haplostemonous, still another indication that diplostemony is ancestral.

The stamens of *Ludwigia* species are much alike externally except for those of sect. *Ludwigia*. In this section, the filament joins the versatile anther in a deep dorsal groove, and the halves of the anther are parallel during development; consequently, the cross section is decidedly H-shaped, unlike that of a developing anther in other sections of the genus (cf. Figs. 3–4).

All the examined ludwigias have a conspicuous endothecium or "fibrous" layer. That is, the hypodermis of the anther is a layer of relatively large cells with narrow wall thickenings. As regards the development of the endothecium, *Ludwigia* anthers are like anthers of *Circaea*, *Hauya*, and certain fuchsias (e.g., *F. arborescens*); they are unlike anthers of *Clarkia*, *Gaura*, and *Gayophytum*, in which the endothecial cells are notably smaller than the epidermal cells. Future studies of onagraceous flowers should take careful note of the anther wall, for there are clear-cut endothecial differences not only among the genera but also within certain genera (*Epilobium*, *Fuchsia*). A prominent endothecium is probably ancestral (see Eames, 1961: 138 ff.); so these differences could turn out to be valuable evolutionary clues.

In my material of *Ludwigia latifolia* and of *L. linearis*, the developing pollen grains are in packets that are separated from other packets above and below by bands of parenchyma. This observation is of more than passing interest because interrupted sporogenous tissue was known heretofore in only five onagraceous genera—*Hauya* and four genera of the tribe Onagreae—and Raven (1969: 161) has argued, contra Munz (1965), that the shared character makes *Hauya* a member of the Onagreae. Discovery of pollen packets in another tribe, where they appear to have evolved twice, undermines Raven's argument and makes *Hauya*'s placement problematic.

PLACENTATION

In certain Ludwigia species, notably those of sect. Oligospermum and Seminuda, the ovules are inserted in 1-seriate rows, one vertical row to each locule (Figs. 5-6). In sect. Ludwigia, Macrocarpon, and Myrtocarpus, pluriseriate ovules are crowded on deeply intrusive placentas that are commonly spatulate in cross-section (Fig. 8). Sections Dantia and Microcarpium also have pluriseriate ovules, but the placentas are not spatulate in cross section (Fig. 9). In L. epilobioides, the ovules are 1-seriate in most locules; they can also be more or less 2-seriate (irregularly so), and both arrangements can occur in the same ovary. Ludwigia hyssopifolia is unusual in that the ovules are irregularly pluriseriate at the distal end of the placentas and 1-seriate below; I have observed the same situation in one collection of L. leptocarpa, sect. Seminuda (Fig. 7). In all its variations, Ludwigia placentation has advanced beyond that of most





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FIGURES 3-8. Ludwigia flowers in cross section.-3. L. alternifolia, Broome 862. Hshaped section of anther. \times 80.—4. L. decurrens, Broome 855. Comparable section. \times 100. In both figs., the abaxial side of the anther is up.-5. L. peploides, Raven 14529. Section passes through two of the five uppermost ovules and through the funicular attachments of the other three. \times 28.—6. L. leptocarpa, Raven 26491. An ovary with all ovules 1-seriate. \times 30. -7. L. leptocarpa, Chevalier 21. Here the upper part of the ovary contains pluriseriate ovules. \times 20.—8. L. foliobracteolata, Raven 21981. Note deeply intrusive placentas. \times 17.

Onagraceae, for one rarely finds a vestige of the ancestral bipartite placental structure, and an actual separation of the ovarian septa (opening of the ventral sutures) can be found only by following them upward into the style (Fig. 11). This reasoning may seem uncritically "classical" to some readers; so I shall take pains to explain.

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If we begin with the formalistic concept of carpel closure endorsed by Eames and others before him, then visualize the divisions of the onagraceous ovary as imbedded carpels and the placentas as fused carpel margins, we can say of Ludwigia that "the fusion is anatomically complete and the placenta is simple in form and structure" (Eames, 1961: 205). To be sure, evolutionary morphologists now find Eames's interpretation of syncarpy inadequate because it does not take into account a change in gynoecial ontogeny that has occurred within many groups, including the Myrtales-namely, a shift in the locus of septal development and ovule inception from discrete carpel primordia to a more recently evolved tubular meristem (the gynoecial cylinder of Sattler, 1973) beneath the carpel primordia. And associated with the origin of the Onagraceae there has been a further modification of the ontogenetic sequence so that the ovules now develop on septa growing upward and inward from a meristematic tube underlying the gynoecial cylinder as well as all the floral primordia (Sattler, 1973). It is not altogether wrong, however, to view the angles formed by the ovarian septa as fused carpel margins, at least in the upper part of the ovary where the septa are ingrowths that actually unite as the ovary develops. After all, the septa do not arise in random positions. They are initiated in line with the ends of the crescent-shaped carpel primordia above them, presumably under the morphogenetic influence of the carpel primordia.³ Moreover, when the developing onagraceous flower first produces septa, then placentas, then ovules within its inferior ovary, it repeats a canalized sequence that began in distant ancestors with superior, apocarpous gynoecia. One cannot argue otherwise, I think, without opting for polyphylesis of angiosperms. As the gynoecium changed from apocarpus to syncarpous and from superior to inferior, the placentas continued to develop from the inner portions of the septa, and the septa continued to develop in vertical alignment with the margins of the increasingly ephemeral carpel primordia. (In Ludwigia, carpel primordia persist only as obscure stigmatic lobes.) From the evolutionary standpoint, therefore, the upper part of the ovary in many Onagraceae does contain carpel margins, even though they are no longer direct outgrowths from the carpel primordia, and the degree to which these margins

at all, the location of the ovary's partition is not fixed. Within a single inflorescence, one may find some ovaries divided in the median plane, others in the tranversal plane (Sattler, 1973).

FIGURES 9-14. Onagraceous flowers in cross section.—9. Ludwigia palustris, Willingham 598. Placentas do not have the swollen appearance of those in Fig. 8. \times 52.—10. Hauya elegans, Breedlove 6432. Ovary of a 5-merous flower showing discrete carpel margins. \times 12.—11. L. octovalvis, Raven 21574. Base of style showing separation of septa; a stamen diverges at right. \times 45.—12. Epilobium fleischeri, cultivated at the Royal Botanic Garden, Edinburgh,

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³ In Lythrum salicaria (Lythraceae), where the two carpel primordia appear fleetingly, if



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as C8092. Uppermost level of ovary showing separation of septa. $\times 53.-13$. Same flower, section taken about 600 μ below Fig. 12 showing median placental grooves. $\times 53.-14$. L. *peruviana*, Steinberg s. n. Level of divergence of floral appendages showing distinct median grooves (arrows) in two of the placentas. $\times 50$.

are fused can be an indication of evolutionary advancement. I have argued elsewhere that the union of carpel margins has reversed to some extent in certain Rosaceae (Eyde, 1975). For angiosperms as a whole, however, I accept the generalization that fused margins are derived and unfused margins ancestral.

To test the applicability of this generalization to the Onagraceae, we can compare gynoecia of the woody tropical genus Hauya with gynoecia of Epilobium, a predominantly herbaceous genus of temperate and cold regions. If we were to take serial cross sections of a Hauya flower and project them rapidly on a screen, proceeding from base to apex, we would see the septa separate within the ovule-bearing region (Fig. 10). If the sections were from a fully developed flower, the radii along which the septa part would be marked by pollen-transmitting tissue. If the projected sections were from a flower of Fuchsia, another woody tropical genus, septal separation would also be observed within the fertile part of the ovary. But a similar sequence through an Epilobium flower would differ in that the septa would not separate, if at all, until we had gone beyond the ovules into the very summit of the ovary (Fig. 12). The ontogenetic explanation for this difference is that the zone of septal upgrowth is relatively greater in Epilobium and the zone of septal ingrowth relatively less (Kaienburg, 1950: 400). Despite the fact that the zone of septal ingrowth is confined to the uppermost part of the ovary in the finished flower of Epilobium, each plane of septal fusion can be followed downward through much of the ovary because its position is marked by a median groove in the placenta (Fig. 13). Similar placental grooves occur in most onagrads, even those with only one ovule per locule, though they are not always as distinct as they are in Epilobium. The taxa I have found to be exceptional—that is, lacking a well-marked placental groove—are Circaea, two species of Oenothera (O. campylocalyx, O. rosea), and most species of Ludwigia. In some species of Ludwigia, such as L. hyssopifolia, an observer passing through the gynoecium from base to apex might enter the style before seeing the separation of the septa, but in certain species of sect. Myrtocarpus and its derivative sect. Ludwigia there is an "elevated disc" below the style (see Micheli, 1875, for illustrations) in which the parting of the septa can be observed. Furthermore, it is only in species belonging to these two sections (L. latifolia, L. peruviana, L. virgata) that I have seen any trace of a placental groove, and then only in the upper part of the ovary (Fig. 14). If my reasoning with regard to ancestral and derived placental characters is correct, these observations place sect. Myrtocarpus near the ancestry of the genus, though its deeply intrusive placentas are advanced over those of most Onagraceae.

If we test the argument by considering the taxonomic distribution of bipartite placentas and partially unfused margins in related families, we find the distribution to be consistent with the view that these features are ancestral. In the Myrtaceae, a family closer than the Onagraceae to the ancestry of the Myrtales, taxa with partially unfused margins within the ovary are found among the capsular groups as well as the fleshy-fruited groups (Ludwig, 1952). In the Lythraceae, the small tree *Lagerstroemia indica* has separate septa in the summit of the ovary, whereas the slender herb *Lythrum salicaria*, a more advanced member

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of the family, has neither separate septa nor grooved placentas (personal observations). Looking into the Sonneratiaceae, Cronquist's (1968) choice as the most nearly ancestral myrtalean family, we find that the septa are separate in the upper fifth of the Sonneratia ovary (Mahabalé & Deshpande, 1957). To judge from published illustrations, the ovaries of Duabanga, the only other genus of the Sonneratiaceae, are structurally similar (Jayaweera, 1967: figs. 1J, 3F). In the highly specialized flowers of Melastomataceae, however, the septa part in the style (van Heel, 1958) or not at all (Eyde & Teeri, 1967; Subramanyam & Narayana, 1969).

DERIVED STATUS OF 4-MERY

The evolutionary morphologist of a few decades ago might have claimed derived status for 4-mery without risking contradiction, at least from American colleagues, on the principle that the "polymerous flower structure precedes, and the oligomerous structure follows from it" (Bessey, 1915). Many exceptions to this principle are known (Stebbins, 1967), however, and Huether's experiments on *Linanthus* (summarized by Stebbins, 1974) have shown how readily the number of floral parts can be increased as well as decreased under selective stress.

In Ludwigia, moreover, higher numbers of floral parts can occur in association with certain advanced features. For instance, in sect. Oocarpon, with 5merous flowers, and in sect. Oligospermum, where 5-mery is the rule and 6-mery occasional, the higher numbers are linked with 1-seriate ovules and a specialized endocarp. In sect. Seminuda, with 4-7-merous flowers, the ovules are also 1seriate, though the fruits are specialized in a different way. Another example is L. epilobioides (sect. Nipponia), a self-pollinating herb of temperate Asia in which 4-6-mery is associated with haplostemony. Raven (1963) reports that 5-merous flowers can be found, albeit rarely, in L. perennis (sect. Caryophylloidea); this species too is commonly haplostemonous. In Myrtocarpus, the "phylogenetically central" section of Ludwigia (Raven, 1963), L. densiflora has 4-6-merous flowers in a spicate (derived) inflorescence, and L. peruviana, in which 5-mery is encountered fairly often, is an aggressive polyploid colonizer. (On the other hand, T. P. Ramamoorthy informs me that 5-mery is the usual condition in the Brazilian shrub L. tomentosa and that he has seen 5-merous flowers in a number of other species belonging to sect. Myrtocarpus.)

Excepting these sections—and sect. *Prieuria* with mostly 3-merous flowers (Raven, 1963)—4-mery is quite constant in the genus *Ludwigia*. I have seen no 4+-merous flowers in sect. *Dantia*, *Macrocarpon*, or *Microcarpium*; and in sect. *Ludwigia*, I have seen only two 5-merous flowers of *L. virgata* and no other exceptions. Throughout the remainder of the family, 4-mery occurs with similar constancy (though the flowers of a few taxa regularly have fewer than four parts). A minority of *Hauya* flowers are 5-merous and five stigmatic rays can occur in *Oenothera* (Cleland, 1972: 6), also in at least one species of *Epilobium* (*E. dodonaei*, personal observation), but I do not know that 5-mery or partial 5-mery has ever been observed in *Fuchsia*, a genus seemingly as close as any to the ancestry of the Onagraceae.

In the Onagraceae, therefore, ancestral status might be claimed for 4-mery

on the grounds that 4+-mery is almost exclusively confined to *Ludwigia*, where it often accompanies derived characters. This reasoning runs into difficulty, however, when the reconstruction of onagraceous ancestry is extended beyond the family limits, for the ancestral Myrtales surely had more than four floral parts per whorl. To claim 4-merous ancestry for the Onagraceae, one would have to begin with myrtalean ancestors in which floral parts were indefinite in number; then postulate a derived group, ancestral to all Onagraceae, with floral parts stabilized in whorls of four; then further postulate a return to 4+-mery in each of several lines within *Ludwigia*. An evolutionary scheme incorporating

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these steps would be less economical than one in which 4-mery is treated as a derived character.

Stebbins (1967) has pointed out that the number of floral parts in a whorl is partly dependent on the number of cells in the floral apex at the time the whorl is initiated; so it is not surprising that higher numbers are often found in larger flowers. The relationship between meristem size and numbers of parts may explain Müller's (1870) observation that individual plants of Brazilian ludwigias (species unspecified) tend to produce 5-merous flowers first, 4-merous flowers later (see also Huether, 1968: 128), but there is no consistent relationship between floral size and merism in *Ludwigia*. Some large-flowered species are constantly 4-merous, whereas *L. torulosa*, with very small flowers, is constantly 5-merous.

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